

Structure and taxonomy of the Carboniferous lycopsid *Anabathra*

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Synopsis

The lepidodendrolean stem, *Anabathra pulcherrima* Witham, is redescribed from permineralized material of the holotype, and its diagnosis emended. Evidence from direct comparison of xylem anatomy and from associated cortex, leaves and megasporangia indicates synonymy with permineralized stems known more commonly as *Lepidodendron brevifolium*, *L. veltheimianum* or *Paralycopodites brevifolius*, over which *A. pulcherrima* has nomenclatural priority. A stem showing both compression and permineralization modes of preservation is described. Its xylem anatomy is indistinguishable from that of *A. pulcherrima*. Its coalified leaf laminae and cuticular features compare both with *A. pulcherrima* and the compression *Ulodendron* Thomas, *non* Lindley & Hutton.

The cones originally attached to *Anabathra* stems are identified as *Flemingites*, with the rhizophore *Stigmaria* the probable rooting organ. A lectotype is selected for the cone *Flemingites scottii* (Jongmans) Brack-Hanes & Thomas. The lepidodendrolean family Flemingitaceae is emended to include the reconstructed '*Anabathra* plant'.

From the specimen described here which shows a combination of permineralization and compression/impression preservation states, it is concluded that *Ulodendron*, *sensu* Thomas 1967 (*non* Lindley & Hutton 1831) is synonymous with *Anabathra* Witham 1833. In addition to the type species, *A. pulcherrima*, the genus also includes two species previously included under *Ulodendron*, *sensu* Thomas, namely *A. thomasiana* sp. nov. and *A. landsburgii* (Kidston) comb. nov. These three species can be distinguished by their differing shapes of leaf bases and the different frequencies of stomata on them.

Introduction

Henry Witham (1830, 1831) was the first palaeontologist to describe and give illustrations of thin sections of permineralized Carboniferous plants prepared by the ground slice method. Using this technique, he examined a wide range of extant vascular plants, as well as jet, some coals, Jurassic and Tertiary woods, and certain British Carboniferous pteridosperms, coniferopsids and lycopsids (Witham 1833). Of the two lycopsid stems, *Anabathra pulcherrima* Witham has received less comment in the subsequent literature than *Lepidophloios harcourtii* (Witham) Seward & Hill. This paper aims to redescribe the neglected holotype material of *A. pulcherrima* rediscovered at the British Museum (Natural History). In the light of new observations and understanding of its structure, the diagnoses of genus and species can be emended.

By making direct anatomical comparisons, and using evidence from associated organs, it is possible to identify this type material with certain permineralized stems from other localities in Scotland, continental Europe and North America. Evidence of organic connexion or association with given genera of cones, dispersed spores and rooting organs has allowed some degree of reconstruction of the plant of which *Anabathra* represents the leafy stem. Given this model for the '*Anabathra* plant', it is interesting to see how it can be incorporated into the present classification of fossil lycopsids which are known from more or less detached organs. In particular, the familial definitions within the Lepidodendrales are in need of some revision. In part, this is a consequence of our varying knowledge of correlations between the vegetative and reproductive organs in lepidodendrolean plants (Thomas 1978).

Further problems in palaeobotany are the recognition and identification, at generic and specific levels, of given organs which have been preserved in different ways. Correlations between compressed and permineralized plants have been found within such taxa as *Sphenophyllum* (Batenburg 1982) and certain Palaeozoic Marattiales (Mosbrugger 1983, Stubblefield 1984), and some instances from the Carboniferous lycopsids are given by Chaloner & Boureau (1967). In looking for the compression equivalent of *A. pulcherrima* it is necessary to consider the relative merits of the methods available for making such comparisons. The conclusions made from these comparisons will alter the classification and naming of certain species, genera and families of fossil plants.

Historical review

The original account of *A. pulcherrima* given by Witham (1831, 1833) is discussed below in the systematic descriptions. The generic name is derived from the Greek ἀνάβαθρον (a seat raised on steps), because the scalariform tracheids resemble steps, and the trivial name refers to the beautifully preserved anatomy of the holotype.

There are few references to *Anabathra* in the subsequent literature, partly as a result of the retention for many years of the type material in private collections. Eleven slides of the holotype were purchased by the British Museum as part of the Nicol Collection in 1867 (Andrews 1980). The manuscript catalogue for that collection describes these slides as '*Cordaites*', '*Sigillaria pulcherrima*', or simply as 'fossil wood'. Features of the anatomy of *A. pulcherrima* given below, along with biostratigraphical considerations, leave only the last of those descriptions still appropriate. One section of the holotype obtained by Williamson (1872a) was purchased by the BM(NH) in 1896, nine more were transferred within the Museum from the Botany Department to the Geology Department in 1898, and the three remaining slides of this specimen were received as part of the Witham Collection in 1940. The holotype slides sent to the Museum National d'Histoire Naturelle, Paris and described by Brongniart (1839), Renault (1879, 1896), and Renault & Roche (1897) have not been traced (personal communication from Dr C. Blanc).

Lindley & Hutton (1835) and Morris (1837) closely compared the secondary xylem of *A. pulcherrima* with that of permineralized *Stigmara ficoides*, a lepidodendrolean rhizophore. However, observations made by Brongniart (1839) and King (1843–45) on the continuous cylinder of exarch primary xylem in *A. pulcherrima* distinguished it anatomically from stigmarian axes. These latter authors drew structural comparisons between *A. pulcherrima* and *Lepidophloios harcourtii* (at that time considered a species of *Lepidodendron*), and suggested the latter may represent the small branches attached in life to *A. pulcherrima*. However, there has been no subsequent evidence to support this suggestion. The production of secondary xylem in *Anabathra* was used by Brongniart to classify it, along with *Sigillaria*, *Stigmara*, the calamites, conifers and cycads, as a gymnospermous dicotyledon. Tate (1853) also compared *Anabathra* with *Sigillaria*, but Renault (1879, 1896) distinguished the latter on its more reduced primary xylem. The primary and secondary xylem of *A. pulcherrima* led Goldenberg (1862) and Schimper (1870) to classify the species within *Diploxylon* Corda. Williamson (1872a) first compared the largely decorticated steles of *A. pulcherrima*, from the Viséan limestone of Pettycur in Scotland, to *Diploxylon cycadoideum* Corda. He suggested that *Anabathra* and *Diploxylon* were probably congeneric, but did not synonymize them since cortical and superficial features were lacking in the material then available to him. However, Williamson (1872b) later described leafy shoots from Pettycur and named them *Lepidophloios brevifolium*. In 1891, he referred this species to *Lepidodendron*, but gave no explanation for making this new combination. Moreover, the name *Lepidodendron brevifolium* had already been used for a stem compression from the Carboniferous of Czechoslovakia (Ettingshausen 1854): Williamson made no reference to these geographically and preservationally different plants, and was presumably unaware of this work of Ettingshausen.

In their account of the permineralized *Syringodendron esnostense* from the Viséan of France,

Renault & Roche (1897) drew close comparisons between that secondarily-thickened, lepidodendralean stem and *A. pulcherrima*. From examination of some holotype slides of *A. pulcherrima* then at Paris, they redescribed the secondary xylem of this species, but misinterpreted the size of the vascular rays as seen in tangential longitudinal section. They also believed the leaf traces supplied branchlets or short spines, but evidence for this is not clear from their illustration. Following Goldenburg and Schimper, Renault & Roche believed this species was very similar to *Diploxylon cycadoideum* Corda, and therefore made the new combination *Diploxylon pulcherrimum* without regard to the nomenclatural priority of *Anabathra* 1833 over *Diploxylon* 1845.

Seward (1910) named leafy shoots from Pettycur *Lepidodendron veltheimianum*, since he considered them identical to the compression/impression species *Lepidodendron veltheimii* Sternberg. Dawson had previously made this comparison, but the identification was denied by Carruthers (Williamson 1872*b*). Williamson agreed with Carruthers in that he believed there was no evidence for the association of the same form of megaspores with *L. veltheimii* compressions as those found with the permineralized *L. brevifolium* in his sense. It will be shown below that the leaf cushions bearing scars of foliar abscission in *L. veltheimii* are distinct from the leaf bases of *Anabathra*.

Although incorrect on both taxonomic and nomenclatural grounds, most permineralized *A. pulcherrima* has been described under the name *Lepidodendron brevifolium* Williamson, non Ettingshausen, or as *Lepidodendron veltheimii/veltheimianum* Sternberg. Scott (1911) and Long (1958) continued to recognize *Anabathra* as a separate genus of lycopsids, but did not compare the specimen from the type locality at Allanbank, Berwickshire with specimens from Pettycur, near Burntisland, Fife. DiMichele (1980) discovered that the supposedly herbaceous lycopsid *Paralycopodites minutissimum* Morey & Morey (1977) represented the lateral branchlets of a larger plant. DiMichele characterized these arborescent plants from American Upper Carboniferous coal balls using both anatomy and morphology, and identified them with *Lepidodendron brevifolium* Williamson from the Scottish Dinantian limestones. Since he demonstrated that they represented a distinct lepidodendralean genus, he placed these stems in the new combination *Paralycopodites brevifolius* (Williamson) DiMichele.

Although the type material of *A. pulcherrima* contains several megaspores, either dispersed or in megasporangia, the first intact cones associated with the species were described from Pettycur (Williamson 1872*b*). Scott (1900) named these cones *Lepidostrobus veltheimianus*, since he believed there was organic connexion in the compression state between this cone and the stem which he called *Lepidodendron veltheimianum*. However, direct evidence for this correlation is lacking. Further, the name *Lepidostrobus veltheimianus* had already been given to a different form of cone (Feistmantel 1873). Therefore, Jongmans (1930) proposed the new name *Lepidostrobus scottii* for the cones associated with leafy shoots at Pettycur. These bisporangiate cones are now generically recombined as *Flemingites scottii* (Jongmans) Brack-Hanes & Thomas (1983). From the six syntypes referred to by Scott (1900) in his description of this species, a cone shown by Williamson (1893: fig. 52) is here selected lectotype of *F. scottii*. This specimen occurs alongside a paratype of the same species (Williamson 1893: fig. 51) in slide number V.8890 of the BM(NH) collections.

At the familial level, Goldenburg (1862) compared *Anabathra* with the Isoetaceae, while Schimper (1870) and Renault (1879) proposed affinity with the Lycopodiaceae (Jongmans 1930). These family names are now used in more restricted senses for two particular groups of herbaceous, lycopsid genera known mostly as living species. The Isoetaceae have no known pre-Permian record, although the Lycopodiaceae date from the Devonian (Chaloner & Boureau 1967). Since *A. pulcherrima* has in most descriptions been named as a species of *Lepidodendron*, its classification has varied from the family Lycopodiaceae *sensu* Brongniart 1828, to the family Lepidodendraceae of the order Lycopodiales *sensu* Potonié 1921, and following Eames (1936) to the family Lepidodendraceae of the lycopsid order Lepidodendrales (Danzé-Corsin 1962). The elevation of the lycopsids to the status of a class of vascular plants (Scott 1909) reflects our greatly increased knowledge of their diversity and peculiarity from the Silurian to the Recent, rather than unwarranted 'inflation of taxonomy' (Harris 1963).

Preservation and palaeoecology

Of the several permineralized axes Witham (1833) originally found at Allanbank, Berwickshire, he sectioned only one to describe *A. pulcherrima*. An unsectioned remnant of the holotype block of this species, V.62010, contains a decorticated stele comparing closely in size and anatomy with the ground slices described and figured by Witham (Figs 1 and 2). Witham described the matrix surrounding the stele as 'carbonaceous clay', but it contains very little fine, inorganic sediment and consists mostly of comminuted plant debris cemented by calcite. He also described the primary xylem (his 'medullary cylinder') as having been largely destroyed owing to replacement by 'siliceous matter'. However, standard mineralogical tests indicate that calcite rather than silica is the main permineralizing agent in the primary xylem, as in the rest of the block. There is no positive evidence for the presence of gypsum in the specimen, as originally described by Witham.

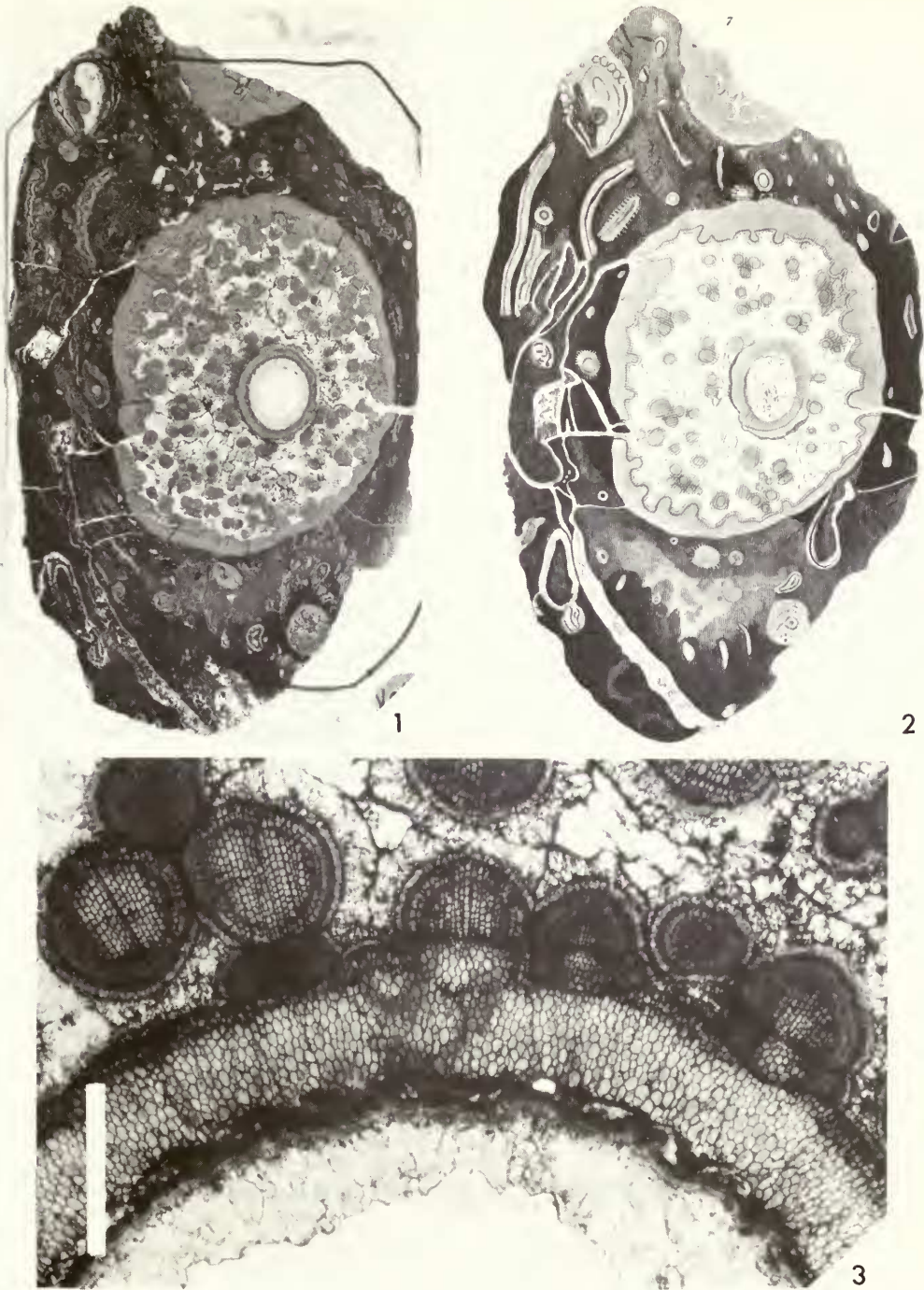
Calcite has been deposited in the holotype material in an unusual way (Witham 1833, Brongniart 1839, King 1845, Williamson 1872*b*). Spheroids of calcite, about 1.0 mm in diameter, are scattered throughout the secondary xylem, while that in the primary xylem is much more homogeneous (Fig. 3). Preservation within the spheroids is such that ornamentation of tracheid walls can be seen clearly, but in the calcite between the spheroids the cell walls are very poorly preserved or absent. There appear to be no particular nuclei for the growth of these calcitic spheroids, and the anatomy of the xylem is quite regular where preserved. This mode of calcite deposition is occasionally seen in plants from other localities in the Calciferous Sandstone Series of Scotland (e.g. Seward 1910: fig. 182). In comparable permineralized plants from the Pettycur limestone or English coal balls, the calcite has been deposited in such a way that their tissues are preserved more continuously. The Allanbank material differs from many coal balls in having less iron pyrites.

The matrix around the holotype contains no evidence of marine fossils, nor are there any remnants of rooting organs. A number of smaller axes, probably of the same species (if not the same individual) as *A. pulcherrima*, occur around the main stele. Some of these retain cortical tissues, but the larger ones tend to be partially decorticated. Several megaspores, both dispersed and in megasporangia, are also found in this matrix, but there are no intact cones. Fragments of fusinized tissue, mainly cortex, also occur here.

From these observations it appears that the limestone was deposited around this plant matter under non-marine conditions. The totally decorticated state of the larger axes indicates that they had probably been transported some distance from their site of growth, a conclusion supported by the lack of rooting organs. Although the fine organic debris may also indicate abrasion of tissues by water transport, such detritus is also typical in coal ball peats, where plant material was apparently deposited quite close to the growth position. Redox conditions reached the level required for the formation of iron pyrites (Perkins 1976). Thus, calcification probably occurred soon after deposition of the plant fragments, or there may have been enough organic matter present to generate highly anaerobic conditions during its decay. The probable source of the calcium carbonate is from dissolution of basalts, since lavas were widely extruded in Fife and Berwickshire during the Viséan (Gordon 1909).

In addition to those axes which are conspecific with *A. pulcherrima*, the matrix around the holotype also contains rachides of the lyginopteridalean pteridosperm *Lyginorachis arberi* (Long 1964) and phyllophores of the stauropteridalean fern *Stauropteris berwickensis* (Long 1966). Witham (1831, 1833) figured *L. arberi*, but he gave it no description or name. Long (1960) recorded the permineralized ovule *Genomosperma latens* from this locality and commented upon its association with *L. arberi* at other localities in the Viséan of Berwickshire. *G. latens* and *L. arberi* occur together in slide V.62016.

The outer cortical tissues of the pteridosperm rachides and fern phyllophores may have been more resistant to abrasion during transport than was the cortex of *A. pulcherrima*. However, there seems no direct means of determining whether these species lived in the same habitat. Comparable associations of pteridosperms and ferns with lycopsids in the Pettycur limestone and in many coal ball floras suggest the possibility that these three groups of plants preserved at Allanbank originated from the same community.



Figs 1–3 *Anabathra pulcherrima* Witham, holotype. Viséan; Allanbank, Berwickshire. Fig. 1, complete transverse section of stele in matrix, V.62011, $\times 1$. Fig. 2, Witham (1833): pl. 8, fig. 7. $\times 1$. Fig. 3, detail of part of primary xylem and innermost secondary xylem in transverse section. Note the discontinuous preservation of cell walls from outer primary xylem outwards. V.62011. Scale bar represents 2.0 mm.

Systematic descriptions

Class LYCOPSIDA Scott, 1909

Order LEPIDODENDRALES Eames, 1936

Family FLEMINGITACEAE Thomas & Brack-Hanes, 1984, emend.

EMENDED DIAGNOSIS. Stems retaining leaf laminae throughout growth, consequently lacking foliar scars. Bisporangiate cones produced, releasing free megaspores and microspores. More than one tetrad produced per megasporangium.

TYPE GENUS. *Flemingites* Carruthers, 1865, emend. Brack-Hanes & Thomas, 1983.

Genus *ANABATHRA* Witham, 1833, emend.

1967 *Ulodendron* Lindley & Hutton, *sensu* Thomas: 778 (this generic usage is different from that of Lindley & Hutton).

1977 *Paralycopodites* Morey & Morey: 67.

1980 *Paralycopodites* Morey & Morey, emend. DiMichele: 1467.

EMENDED DIAGNOSIS. Stems with single, exarch protosteles, protoxylem uniformly distributed at margin, medullated except at most distal levels. Lateral branchlets formed without associated gap in protostele of main stem. Outer primary cortex homogeneous, composed of thick-walled, longitudinally elongate cells. Outer secondary cortex (periderm) homogeneous, retaining distinct leaf traces. Stem surface bearing straight, linear leaves, spirally arranged in evident parastichies; leaf laminae retained following secondary growth of xylem and cortex in stem. Leaf bases with stomata.

TYPE SPECIES. *A. pulcherrima* Witham 1833, emend.

Anabathra pulcherrima Witham 1833, emend.

1831 'Fossil plant found at Allenbank'; Witham: pl. VI, fig. 7 (t.s. of part of secondary xylem.)

1833 *Anabathra pulcherrima* Witham: 39–42; pl. VIII, figs 7–12; pl. XVI, fig. 7.

1850 *Stigmaria anabathra* Corda; Unger: 227–228. (Unger's material differs from the type material described under this name by Corda).

1862 *Diploxylon anabathra* Goldenberg: 24.

1869 *Ulodendron minus* Lindley & Hutton; Carruthers: 227; pl. XXXI, figs 1–4. (This specimen differs in structure from the type material of *U. minus* L. & H.).

1872a *Diploxylon*; Williamson: 240.

1872b *Lepidophloios brevifolium* Williamson: 310; pl. XLIII, figs 20–2.

1886 *Lepidodendron selaginoides* Sternberg; Felix: 32–35; pl. II, fig. 3. (Misidentified leaf from German coal ball.)

1891 '*Lepidodendron brevifolium* Burntisland Form' Williamson: 58. (A homonym of a different species of Ettingshausen, 1854).

1897 '*Diploxylon pulcherrimum* de Witham'; Renault & Roche: 15–16; pl. VIII, fig. 5.

1910 *Lepidodendron veltheimianum* Sternberg; Seward: 177; text-figs 186A, B. (Comparison with the stem compression *Lepidodendron veltheimii* Sternberg).

1977 *Paralycopodites minutissimum* Morey & Morey: 64–69; pl. 1, figs 1–10; pl. 2, figs 11–19.

1980 *Paralycopodites brevifolius* (Williamson) DiMichele: 1467; figs 1–16.

EMENDED DIAGNOSIS. Leaf bases greater in length than breadth. About 350–400 stomata/mm² on leaf bases.

HOLOTYPE. Hand specimen, V.62010, and slides prepared from this, V.62011–33.

LOCALITY AND HORIZON. Allanbank, near Allanton, Berwickshire, Scotland. National Grid Reference: NT 864545. ('Allen-Bank' of Witham 1831, 1833; see Long 1958 for details of this site). This part of the Cementstone Group of the Calciferous Sandstone Series has been assigned a Viséan 1 or uppermost Tournaisian age within the Lower Carboniferous (Dinantian) on the basis of palynology (Meyer-Berthaud 1984).

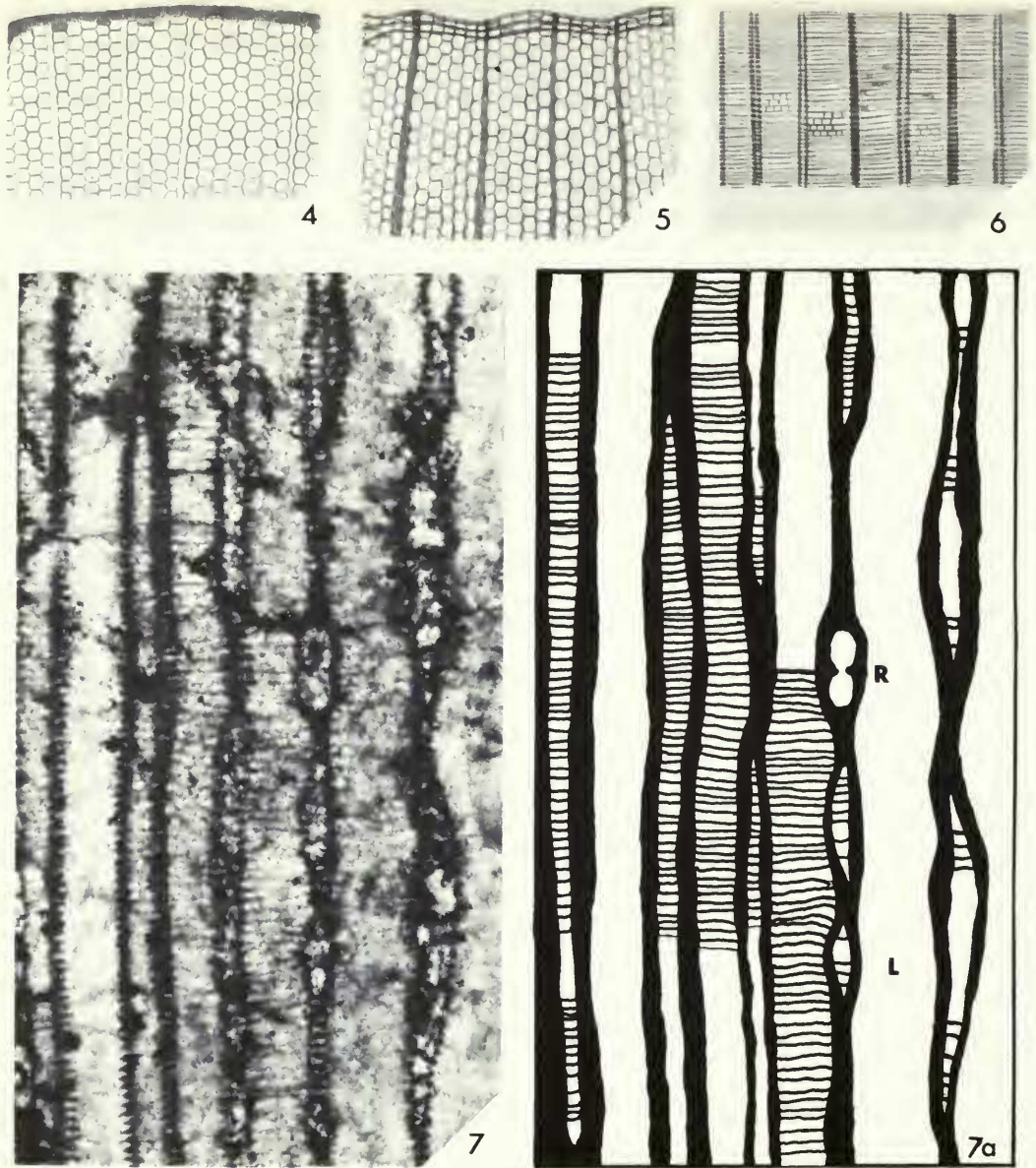
DESCRIPTION OF HOLOTYPE. Although Witham first illustrated part of the xylem of *A. pulcherrima* in 1831, he gave neither a detailed description nor the name until 1833. The original block from which a number of ground slices were prepared contained the stele of *A. pulcherrima* in the form of a truncated cone. Although Witham stated that the axis was laterally compressed, the generally undistorted preservation of the xylem indicates that the stele may have originated from part of the crown where dichotomous branching gave rise to oval rather than terete steles as seen in transverse section. The apex of the truncated cone was rounded, and measured about two-thirds of the basal diameter, but Witham gave no absolute dimensions for the unsectioned axis. Since the remaining block, V.62010, matches the larger sections prepared from the original in the size and position of the holotype axis, it presumably represents the base, with an overall diameter of about 70 mm. Witham described transverse features, at intervals of about 50 mm, interrupting the longitudinal striations seen on the surface of the axis. None of these transverse markings are visible in the remaining block, nor in the longitudinal sections prepared from the original. I agree with Witham that they do not represent constrictions or expansions in the preserved tissue, as seen in many sphenopsids, but are simply fractures passing through both fossil and matrix. Such disruptions can be seen in some of the transverse sections (Figs 1 and 2).

At the centre of the holotype axis there is a mass of apparently homogeneous calcite, between 8 mm and 10 mm in diameter, usually with a central space or gap (Fig. 3). This calcite is surrounded by a cylinder of primary xylem. It is uncertain whether the metaxylem tracheids formed continuous tissue to the centre of the stele in the life of the plant, composing a solid protosteles as, for example, in *Lepidodendron rhodumnense*. Instead, there may have been a wholly parenchymatous medulla encircled by primary xylem (as in *Lepidophloios harcourtii*), or possibly there was a 'mixed pith' of tracheids dispersed amongst parenchymatous cells (as in *Diaphorodendron vasculare*). If there existed a solid protosteles, it is difficult to explain why none of the inner tracheids have been preserved, given that the same block includes xylem with very well preserved tracheids. Similarly, with a 'mixed pith' one would expect to find a few tracheids preserved in this part of the stele. With a medullated protosteles, however, it is much more likely that the parenchymatous tissue would have collapsed or been degraded during sedimentation, or broken down while the plant was still alive. (Williamson, 1872a, and DiMichele, 1980, have described other specimens of *A. pulcherrima* which have a well-preserved, entirely parenchymatous medulla.)

Witham gave no description of the primary xylem, even though in the holotype this is as well preserved as the secondary xylem. In describing his 'central medullary cylinder', Witham's figures of radial files of thick-walled cells showing hexagonal transverse sections are clearly part of the secondary xylem (Fig. 4). Primary xylem forms a continuous ring within the secondary xylem, up to 2.2 mm in radial thickness (Figs 1 and 3). Metaxylem tracheids are polygonal in transverse section, up to 360 μm in diameter and at least 540 μm in length, although no distinct end walls were encountered. As King (1845) commented, the flexuous shape of these tracheids means they exceed the length apparent in any one longitudinal section. The metaxylem tracheids show scalariform thickenings on all their walls, the transverse bars being about 6 μm apart; these bars sometimes anastomose, and in places are joined by minute fimbrials. The fimbrials, considered by some authors as diagnostic for the Lepidodendrales, but certainly unknown outside the Lycopsidea, were figured by Witham from the secondary xylem tracheids (Fig. 6), although I have not observed them in the available holotype sections. Protoxylem tracheids are distributed more or less evenly in a continuous zone around the outer margin of this exarch protosteles (Figs 3 and 8). They are about 30 μm in diameter, but the form of wall thickening is not clear in this material.

Secondary xylem immediately surrounds the primary xylem, reaching a maximum radial thickness of 23 mm in this specimen. There is no indication of growth rings. Tracheids quadrilateral or hexagonal in transverse section and up to 155 μm in diameter (Figs 3-5, 8) occur. Their longitudinal walls show essentially the same form of scalariform thickening as in the metaxylem. No distinct end walls are visible for secondary xylem tracheids, but many incomplete lumina between 5 mm and 10 mm in length were measured.

Vascular rays can be seen crossing the secondary xylem in tangential longitudinal section



Figs 4-7a *Anabathra pulcherrima* Witham, holotype. Figs 4-6, Witham (1833): pl. 8, figs 8, 9 & 10 respectively; all $\times 100$. (These figures cannot be assigned to any particular slide of the holotype material.) Figs 4 & 5, secondary xylem in transverse section. Fig. 6, secondary xylem tracheids in tangential longitudinal section. Fig. 7, tangential longitudinal section of secondary xylem, V.62017. $\times 105$. Fig. 7a, interpretive drawing of Fig. 7, showing apparent vascular ray to left of **R**, as distinct from sections of undulating tracheid walls where lumina of tracheids are partly obscured by scalariform bars, as immediately to left and right of **L**.

(Figs 7, 7a). The generally undistorted form of the stele makes it unlikely that these rays are only intercellular disruptions as suggested by Witham. They are up to $90\ \mu\text{m}$ wide, and appear to be between $100\ \mu\text{m}$ and $160\ \mu\text{m}$ in height. Little cellular material remains in the vascular rays, but in some areas fragments of cell walls remain (Fig. 7). The longitudinal walls of the secondary xylem tracheids often undulate, repeatedly passing in and out of the plane of section.

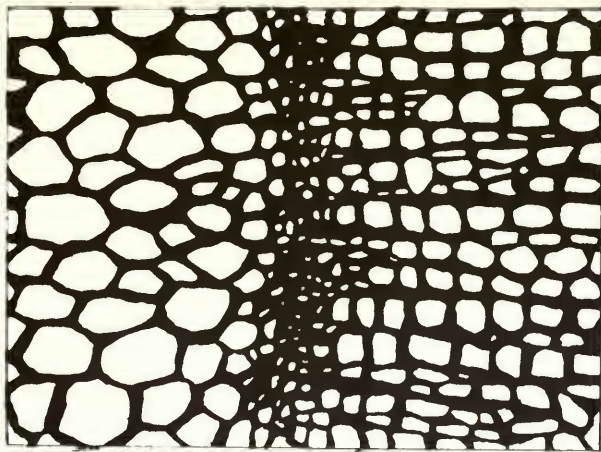


Fig. 8 *Anabathra pulcherrima* Witham, holotype. Detail of part of junction between primary xylem and secondary xylem as seen in transverse section. Note the smallest diameter tracheids, the protoxylem, arranged continuously between the large, irregularly positioned metaxylem tracheids and the radially arranged secondary xylem tracheids. V.62011, $\times 28$.

In some places, this may give rise to apparently taller vascular rays. However, the presence of at least a few transverse bars crossing these 'rays' shows that they are only incomplete sections of the lumina of adjacent tracheids (Fig. 7a).

In a tangential longitudinal section of the secondary xylem, Witham figured a leaf trace (Figs 9 and 10). These traces, which Witham referred to as 'medullary rays', are up to $250\ \mu\text{m}$ wide, and about $450\ \mu\text{m}$ in height; poor preservation of the parenchymatous cells makes their limits indistinct. Scalariform tracheids, $20\ \mu\text{m}$ to $30\ \mu\text{m}$ in diameter, fill the central part of the leaf trace. Some can be seen in connexion with the protoxylem.

In one section, V.62032, there is evidence of lateral, pseudomonopodial branching of the axis. Just outside the main stele is a smaller, decorticated stele sectioned in the same plane. It consists of solid, primary xylem surrounded by secondary xylem, except on its surface adaxial with respect to the larger stele (Fig. 12). The overall crescentic shape of this smaller stele, and its position in relation to the main stele, indicate that it is probably a lateral branchlet. In none of the available sections of the holotype is there any disruption of the main axis which can be related to the formation of this or other lateral branchlets.

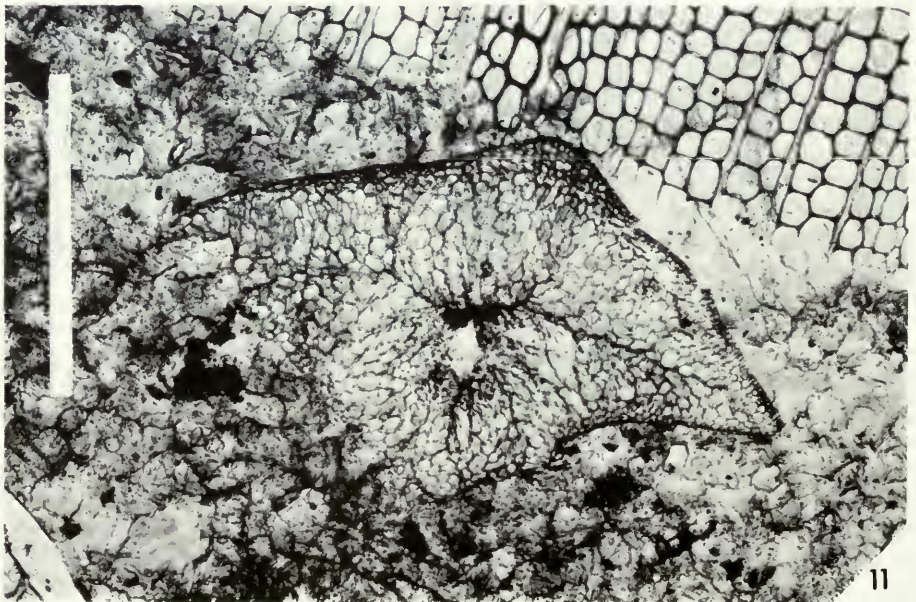
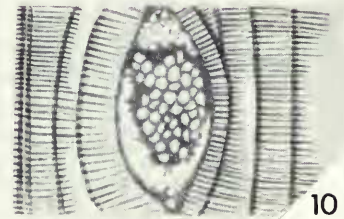
The width of secondary xylem compares closely with that of steles from large branches or the main trunk of arborescent lycopsids. As there are no extraxylary tissues preserved attached to the holotype stele, the total diameter of the original stem remains unknown.

In addition to the pteridosperm and fern organs mentioned above, the holotype of *A. pulcherrima* is surrounded by several other organs which show anatomical details of greater similarity to the holotype, and which are probably conspecific with it.

In Witham's original figure of the entire stele of *A. pulcherrima* there are shown at least two other decorticated steles showing xylem with the same structure as that of the holotype (Figs 1, 2). This anatomical comparison is supported also by longitudinal sections with both holotype and associated steles together (e.g. V.62022); although the quality of preservation and the number of available characters for comparison are limited, there are no structural differences visible to deny identity between these steles and the *A. pulcherrima* holotype. The matrix also contains a number of stems, about 5 mm to 15 mm in diameter, which retain varying amounts of outer primary cortex; they all contain single steles with only primary xylem. The steles are exarch, with the protoxylem arranged evenly and continuously around the metaxylem, giving a smooth outline to the stele in transverse section. In those steles greater than 1.5 mm in diameter, there is a hollow at the centre of the metaxylem, probably indicating medullation of the



Figs 9–11 *Anabathra pulcherrima* Witham, holotype. Fig. 9, leaf trace seen in tangential longitudinal section of secondary xylem. V.62017. Scale bar represents 240 μm . Fig. 10, Witham (1833): pl. 8, fig. 12; leaf trace as seen in Fig. 9 (not assignable to any particular slide of the holotype). $\times 100$. Fig. 11, isolated leaf lamina seen in transverse section in matrix around main stele. V.62015. Scale bar represents 1.0 mm.



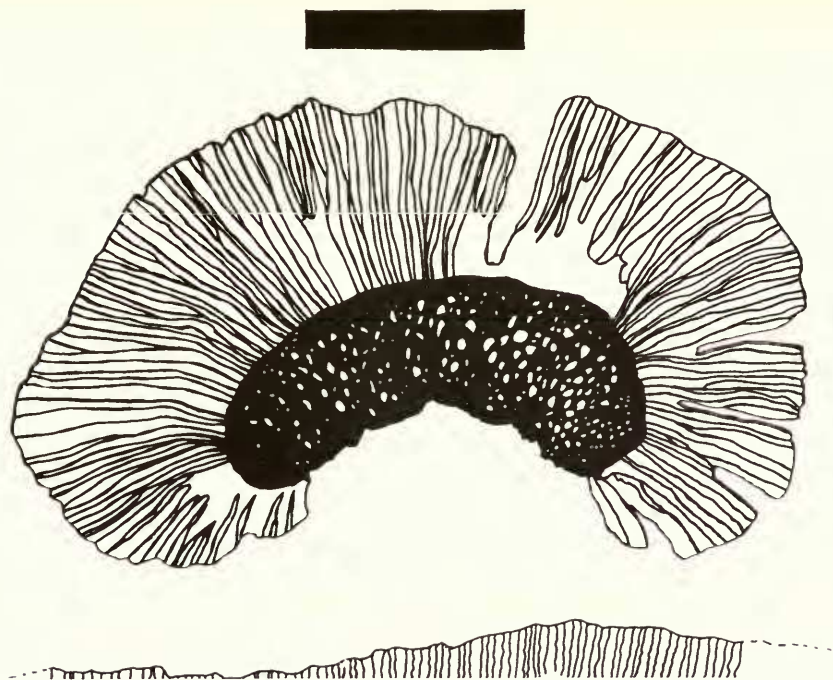


Fig. 12 *Anabathra pulcherrima* Witham. Stele of probable lateral branchlet seen in transverse section, closely associated with *A. pulcherrima* holotype. Note the eccentric, radiating files of secondary xylem tracheids surrounding the primary xylem except on its adaxial surface, opposite the scale bar. V.62032. Scale bar represents 2.0 mm.

stele. There is a gap between the protoxylem and the outer primary cortex, and the latter has often collapsed laterally around the stele. Occasionally, minute bundles of tracheids occur in this gap, probably remains of leaf traces. Outer primary cortex is preserved up to 2.5 mm wide, and is composed of a homogeneous prosenchyma of thick-walled stereids up to 90 μm in diameter and at least 450 μm long. Cortical cell diameter decreases towards the outer part of the axis, and the outermost cells appear to be shorter as seen in oblique section. In some of these stems, the cortical tissue contains rounded or oval hollows, occasionally enclosing a few obliquely sectioned, scalariform tracheids, indicating that they are leaf traces. There is no secondary growth in the cortex of these stems, and no clear leaf bases or epidermis can be seen.

Although it is difficult to compare stems with and without secondary growth, or between corticated and decorticated states, the metaxylem anatomy, arrangement of the protoxylem, and probable medullation of these smaller stems also compare so closely with the holotype stele that they are probably conspecific.

Leaf laminae, leaf bases and secondary cortex also occur in the matrix around the *A. pulcherrima* holotype. In some instances, the leaf bases are attached to secondary cortex (Fig. 13). The secondary cortex appears homogeneous across a radial thickness of 3.7 mm. The cells of this tissue are in radial files, and are rectangular in transverse section, measuring up to 20 μm radially and 36 μm tangentially. Although leaf bases and secondary cortex are in organic connexion, no leaf traces can be seen crossing the secondary cortex in the type material. In transverse section, the leaf bases appear as winged structures, extending up to about 2 mm from the outside of the secondary cortex, and about 2.5 mm in tangential width. No ligules or their pits have been found in these leaf bases. The wings of the leaf bases do not overlap tangentially. Since the leaf lamina remains attached to the stem, even after secondary growth of the cortex, it is difficult to distinguish features of the leaf base from those of the leaf lamina. The cortical cells

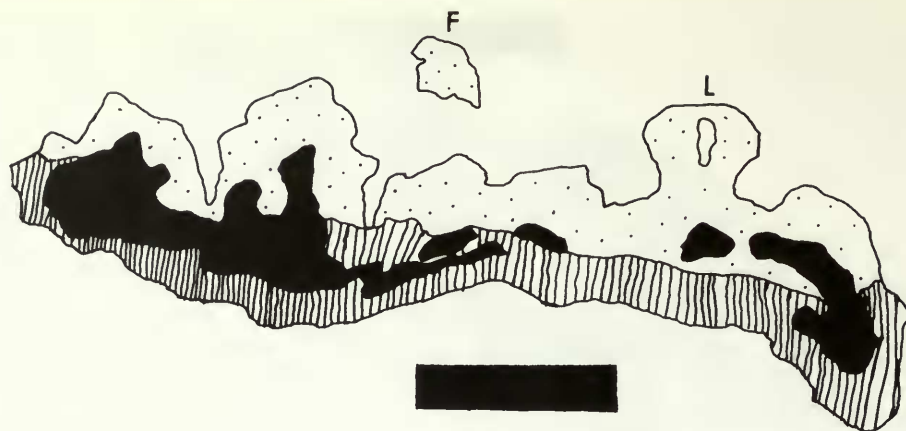
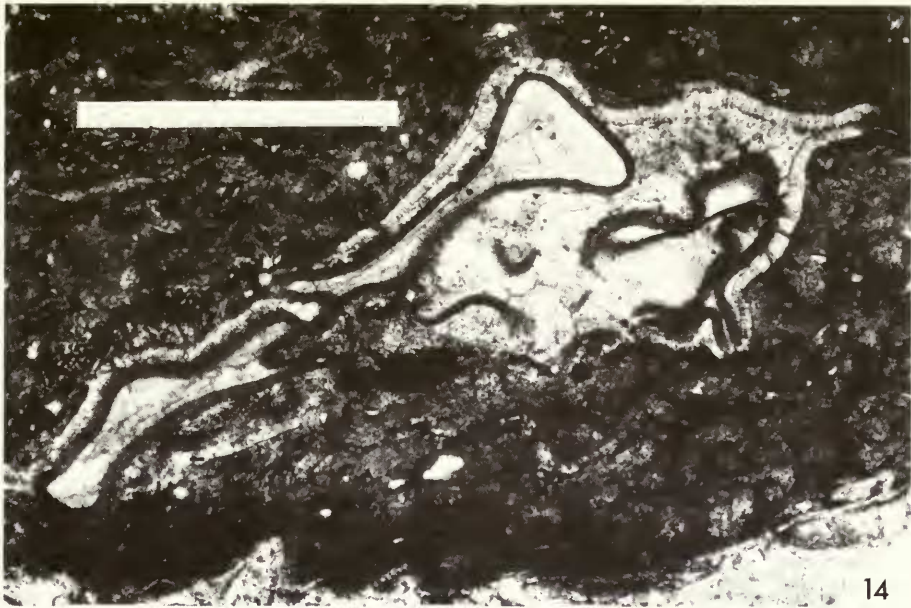


Fig. 13 *Anabathra pulcherrima* Witham. Transverse section of a fragment of outer cortex, closely associated with *A. pulcherrima* holotype. Note the secondary cortex (radially striated), the primary cortex of the leaf bases (stippled), some indication of leaf lamina retention (L), and an associated, free leaf lamina (F). Black shading represents destruction of cells by mineralization. V.62016. Scale bar represents 3.0 mm.

of the leaf bases are thick-walled and approximately isodiametric, about $30\ \mu\text{m}$ to $50\ \mu\text{m}$ across. Epidermal tissue is not preserved on the leaf bases, but the outermost tissue present is a hypodermis of thick-walled cells which lie parallel to the length of the leaf. No parichnos is visible in the available type material.

Isolated leaf laminae occur in the matrix sectioned in various planes (Fig. 11). In transverse section the leaves are rhomboidal, becoming triangular in section distally. Leaves vary from 1.5 mm to 2.5 mm in width, and are about 1.0 mm high. Leaf traces about $25\ \mu\text{m}$ in diameter consist of up to ten tracheids, but there is a gap between the xylem and the innermost mesophyll. The mesophyll cells are thick-walled, closely packed, polyhedral, and up to $90\ \mu\text{m}$ in diameter. The outermost preserved tissue is a continuous hypodermis, two to four cells thick, consisting of thick-walled cells arranged most numerous at the adaxial crest and abaxial keel of the leaf. Although no epidermis is preserved in the more intact leaves, a number of fragments of hypodermis probably originating from the same form of leaf occur in the matrix. These fragments sometimes show epidermal features such as stomata, but the preservation in this material is too poor for detailed description or illustration here.

Dispersed through most of the holotype sections of *A. pulcherrima* are several spiny megaspores (Fig. 15). From eleven such megaspores sectioned in several different planes, the range in equatorial diameter is 0.85 mm to 1.65 mm, with a mean value of 1.28 mm. The megaspores have a gula up to $50\ \mu\text{m}$ tall and about $200\ \mu\text{m}$ in width (Fig. 16). The exine varies between $15\ \mu\text{m}$ and $35\ \mu\text{m}$ in thickness, $20\ \mu\text{m}$ being a typical value. Spines occur more densely on the distal surface where their bases may be only $40\ \mu\text{m}$ apart. The spines are about $100\ \mu\text{m}$ long, are slightly swollen at the base, but taper little along their length from a width of $14\ \mu\text{m}$. Spine apices are blunt. Nearer the gula, spines occur less densely, are generally shorter, and are usually reflexed. These features agree with the dispersed megaspores called *Lagenicula subpilosa* (Ibrahim) Potonié & Kremp, the rather large size of the spores falling within the range of the major form of the species (Dijkstra 1952). Among other *Lagenicula* species of similar age and geographical distribution, *L. horrida* Bennie & Kidston ex Zerdnt (1934) and *L. crassiaculeata* Zerdnt (1934) compare closely with these *in situ* megaspores. However, *L. horrida* has a more sparse covering of spines than has *L. subpilosa*; the spines of *L. horrida* taper progressively from their bulbous base to their pointed apex. The spines of *L. crassiaculeata* are of a similar surface density to those of *L. subpilosa*, but the longest exceed $180\ \mu\text{m}$; the gula of this species may be up to $800\ \mu\text{m}$ in height. Chaloner (1953a) obtained *L. crassiaculeata* megaspores from the cone compression *Flemingites allantonensis* (Chaloner) Brack-Hanes & Thomas.



14



15

Figs 14–15 Megasporangium and megaspore associated with holotype of *Anabathra pulcherrima* Witham. Fig. 14, oblique section of megasporangium containing spores and showing prismatic cells of sporangium wall. Attributable to *Flemingites scottii* (Jongmans) Brack-Hanes & Thomas. V.62012. Scale bar represents 1.0 mm. Fig. 15, oblique section of dispersed megaspore, attributable to *Lagenicula subpilosa* (Ibrahim) forma *major* (Dijkstra ex Chaloner) Potonié & Kremp. V.62015. Scale bar represents 240 μm .

In some instances, up to four megaspores have been sectioned still within the megasporangium (Figs 14 and 16). There is no evidence of abortive spores, but the size of the megasporangia indicates that they could have contained more than one tetrad of megaspores. The prismatic cells of the megasporangium wall are occasionally visible (Fig. 14). These cells are thin-walled, about 35 μm across radially and about 10 μm tangentially. No other cells are seen

within the intact megasporangia, and there are no microsporangia, sporophylls or intact cones in the available holotype material.

DISCUSSION. DiMichele (1980) emended the generic diagnosis of *Paralycopodites* Morey & Morey 1977, showing that what had first been considered a genus of herbaceous lycopsids were arborescent, lepidodendralean stems bearing deciduous, leafy, lateral branchlets. He specifically identified these stems from American Upper Carboniferous coal balls with material of *Lepidodendron brevifolium* Williamson from Pettycur, for which he designated a lectotype from that Scottish, Lower Carboniferous locality. DiMichele distinguished *Paralycopodites* from other lepidodendralean stem genera on such features as its persistent leaves, and its homogeneous outer primary cortex and periderm of thick-walled prosenchyma. As seen in transverse section, the smooth margin of the protostele differs from all known lepidodendralean steles except that of *Bothrodendron*, known only from Czechoslovakian and English coal balls (Williamson 1889; personal communication from Prof. K. V. Leistikow and Frl. Ulrike Bertram of Frankfurt). The deciduous, lateral branchlets are not peculiar to *Paralycopodites* since 'ulodendroid' scars which remain on the stem after these branchlets are abscised are also known in *Lepidodendron*, *Bothrodendron* and *Lepidophloios* (Jonker 1976). Given that *P. brevifolius* is based upon a lectotype from the original material of Williamson, it is interesting that Williamson closely compared *L. brevifolium* to *A. pulcherrima* Witham. To quote Williamson (1872a: 227):

... we have, at once, the closest resemblance to WITHAM's *Anabathra* and CORDA's *Diploxyton*, as well as to those now under consideration. That WITHAM's plant is identical, in type, with mine, is further indicated by his tab. 8 fig. 12, where he exhibits one of the large compound medullary rays shown in my Plate XXVII fig. 23.

Similarly, Williamson (1872b: 310, footnote):

Until the very characteristic macrospores of my plant are shown to exist in some of the localities in which *Lepidodendron Veltheimianum* is common, I think it best to retain my proposed provisional name. I find these macrospores associated with a section of WITHAM's original specimen of *Anabathra pulcherrima*, for which I am indebted to Professor KING, and have not a doubt that the latter is identical with the Burntisland plant; but I have not sufficient proof to establish this point with the certainty requisite for a scientific determination.

From the description of the holotype of *A. pulcherrima* given above, there is clearly identity in xylem anatomy, and no essential differences in structure, between this species and the

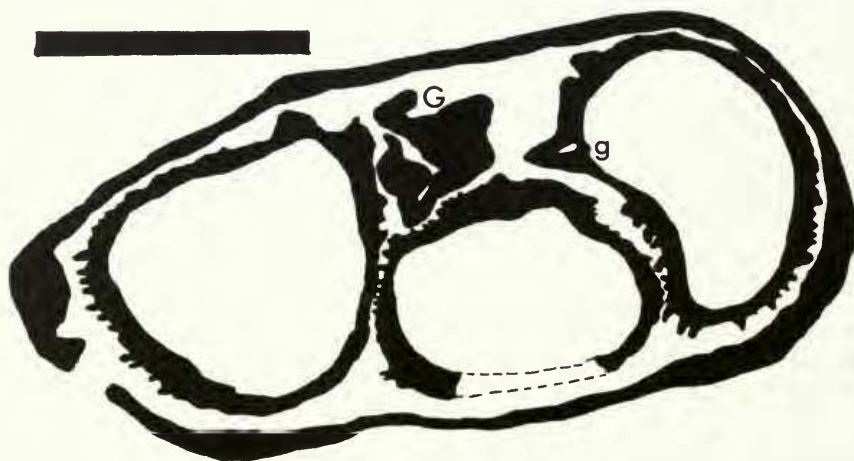
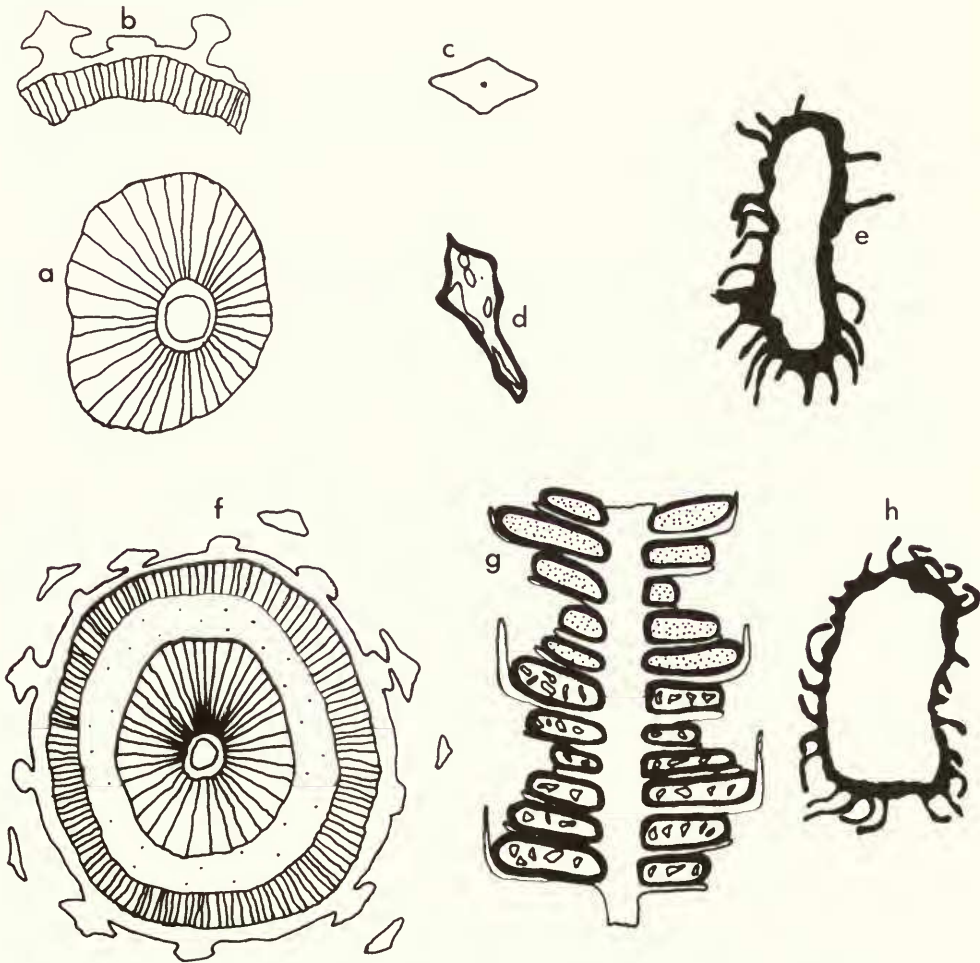


Fig. 16 Megasporangium associated with the holotype of *Anabathra pulcherrima* Witham. Oblique section, but probably close to tangential longitudinal plane of original, intact cone. Note apical gula structures of megaspores in transverse (G) and longitudinal (g) section. V.62018. Scale bar represents 1.0 mm.

material named *P. brevifolius*. Indirect evidence from the smaller stems with cortex, the secondary cortex with attached leaves, and isolated leaf laminae closely associated with the holotype of *A. pulcherrima* lend further support for the specific identification with *P. brevifolius*. Further, the megasporangia containing *Lagenicula subpilosa* associated with the holotype of *A. pulcherrima* are identical to the megasporangia of the cone *Flemingites scottii* associated with *P. brevifolius* at Pettycur. These structural comparisons between the various organs associated with *A. pulcherrima* at Allanbank and at Pettycur are summarized in Fig. 17.



Figs 17a-h Comparison of permineralized, Viséan lycopsid fossils from Allanbank, Berwickshire, with similar organs from Pettycur, Fife. Figs 17a-e, holotype of *Anabathra pulcherrima* Witham and associated organs from Allanbank. a, holotype stele in transverse section, $\times \frac{2}{3}$; b, transverse section of outer cortex with leaves attached, $\times \frac{2}{3}$; c, detached leaf lamina in transverse section, $\times 5$; d, oblique section of megasporangium, $\times 10$; e, oblique section of a megaspore referable to *Lagenicula subpilosa* (Ibrahim) forma *major* (Dijkstra ex Chaloner) Potonié & Kremp, $\times 40$. Figs 17f-h, comparable lycopsids from Pettycur. f, transverse section of *Paralycopodites brevifolius* (Williamson) DiMichele, stem with attached and associated leaf laminae, $\times \frac{2}{3}$; g, radial longitudinal section of part of *Flemingites scottii* (Jongmans) Brack-Hanes & Thomas, bisporangiate cone, $\times 2.5$; h, oblique section of a megaspore referable to *Lagenicula subpilosa* (Ibrahim) forma *major* (Dijkstra ex Chaloner) Potonié & Kremp, $\times 40$.

Given the quality of preservation of the *A. pulcherrima* holotype, there is identity in structure between this and the lectotype of *P. brevifolius*. Under the International Code of Botanical Nomenclature (Voss 1983), Article 11.3 requires that *Anabathra pulcherrima* Witham take priority over *P. brevifolius*, and is the validly published and legitimate name for this fossil species.

Anabathra landsburgii (Kidston 1893), comb. nov.

1968 *Ulodendron landsburgii* (Kidston) Thomas: 425–428; figs A–D. (See this reference and Crookall (1964) for further synonymy, typification, locality, age, description, and remarks).

EMENDED DIAGNOSIS. Leaf bases greater in length than breadth. About 200 stomata/mm² on leaf bases.

Anabathra thomasiana sp. nov.

1967 *Ulodendron majus* Lindley & Hutton; Thomas: 778–779; figs 1, A–D. (See this reference and Crookall (1966) for further synonymy, locality, age, description and remarks, excluding *U. majus*, *sensu* Lindley & Hutton 1831 only.)

DIAGNOSIS. Leaf bases greater in breadth than length. About 450–500 stomata/mm² on leaf bases.

HOLOTYPE. Specimen L.70, with eight slides of cuticle preparations made from it, of the Bradford Metropolitan Museums Service collection at Cliffe Castle Museum, Keighley, West Yorkshire.

NAME. The epithet *thomasiana* is used here to commemorate the work of Dr Barry A. Thomas on the type of this species.

Comparison of *Anabathra* with *Ulodendron*

Lindley & Hutton (1831) established the name *Ulodendron* for stem compressions showing rounded, concave scars in longitudinal series, and with contiguous leaf bases in oblique rows. They named two species, *U. majus* and *U. minus*; Andrews (1955) designated *U. majus* as the type for the genus. Crookall (1966) and Jonker (1976) stated that the holotype material of *U. majus* Lindley & Hutton has apparently been lost, and a neotype specimen has been proposed by Crookall. The original description and figure of the *U. majus* holotype are not sufficiently detailed for other specimens to be readily identified with it. Indeed, Jonker demonstrated that the large scars on this holotype occur also on certain other lepidodendrolean stem genera, and hence these scars alone do not serve to diagnose *Ulodendron* Lindley & Hutton as a distinct genus. Since its surface features differ in size only, *U. minus* is generally regarded as a synonym of *U. majus* (Crookall 1966). However, Jonker identified the neotype specimen of *U. majus* with *Lepidophloios laricinus* Sternberg 1825, thereby casting further doubt upon the generic distinction of *Ulodendron* Lindley & Hutton. As with the drawing and description of the lost holotype of *U. majus*, foliar details are very poor in the neotype specimen of that species, since it is in the form of an impression counterpart. Little would be gained by perpetuating the use of this confused and poorly typified generic name by applying it to specimens with evident 'ulodendroid' scars, but lacking in foliar detail.

Thomas (1967) described a compression specimen of the outer cortex of a stem on which linear leaf laminae were apparently still attached to rhomboidal leaf bases in oblique rows. He named this specimen *U. majus* Lindley & Hutton, and emended the diagnoses of the genus and species to include details of the leaves and cuticular preparations. This specimen differs from the holotype of *U. majus* in showing leaf laminae in close association, suggestive of organic connexion, and in having four distinct angles to the rhomboidal leaf bases. It is difficult to compare the features of the inner surface of detached cortex described by Thomas with the details of the external surface of the stem figured by Lindley & Hutton (1831: pl. 5). Thus, for example, it is not clear that the grooves between the leaf cushions described from the specimen

of Thomas compare with the apparently contiguous leaf bases or cushions shown by Lindley & Hutton. It is also uncertain from the holotype illustration of *U. majus* whether leaf laminae had been retained or shed. The emended diagnosis given by Thomas for *Ulodendron* could thus more usefully be applied to a new generic name encompassing *Ulodendron*, *sensu* Thomas 1967, *non* Lindley & Hutton 1831.

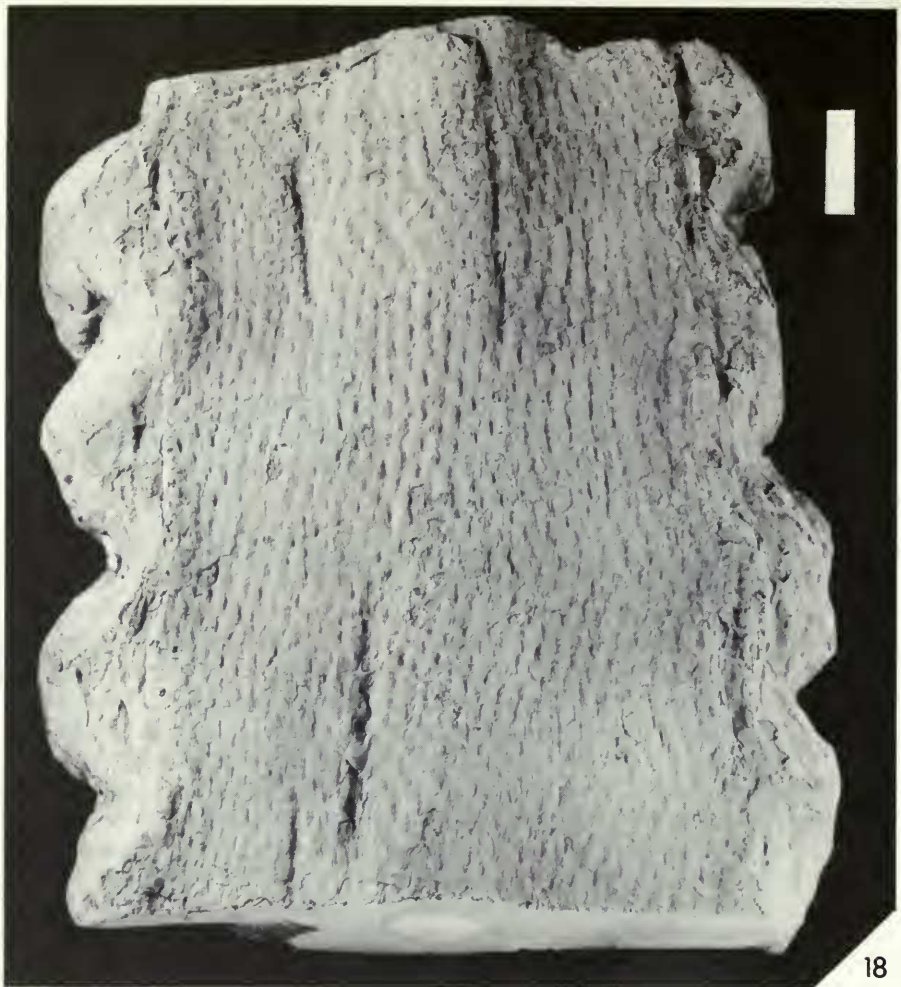
From the observations of Thomas, it is clear that the retention of leaf laminae on a stem large enough to show 'ulodendroid' scars distinguishes his specimen from all other described genera of lepidodendrolean stem compressions. DiMichele (1980) compared *Ulodendron*, *sensu* Thomas, with the permineralized stem he called *Paralycopodites*, here regarded as a synonym of *Anabathra*. DiMichele did not unite these genera because he believed the anatomy of *Ulodendron* to be unknown.

Williamson (1872a) described a permineralized stem which he named *Ulodendron* on the basis of its lateral branch scars. The anatomy of the xylem and the cortex, and the broad leaf cushions bearing scars of foliar abscission seen in this specimen, indicate closer affinities with *Lepidophloios* than with *Ulodendron*, *sensu* Thomas.

Carruthers (1869) briefly described an unusual but most significant specimen from the Westphalian of Yorkshire, now in the BM(NH) collections. (The parts of this specimen are registered under V.62037-41, with accompanying microscope slides. Two other '*Ulodendron*' specimens, V.282 and V.5987, show the same combination of modes of preservation. However, both of these retain very poorly preserved xylem, and only V.5987 yields cuticle.) This shows a permineralized xylem cylinder, a cortical cavity largely infilled with ferruginous shale, and a compressed, coaly surface (Figs 18, 18a). The specimen has two opposite rows of alternating, rounded, concave scars, and Carruthers used these features to identify it as *Ulodendron minus* Lindley & Hutton. The xylem has been preserved by a combination of calcite and pyritic permineralization, and peel sections were prepared from it. Exarch primary xylem forms what appears to have been a continuous cylinder in life (Fig. 19). From the approximately uniform thickness of the preserved primary xylem, it appears that the protosteles were probably medullated in life. To one side of the oval protostele there is an outward bulge without evident disruption to the nearby secondary xylem, suggestive of unequal dichotomy of the stele. The metaxylem tracheids are polygonal in transverse section and vary between 100 μm and 150 μm in diameter. The protoxylem tracheids are arranged evenly and continuously around the outer margin of the primary xylem. The surrounding secondary xylem is generally more pyritized than the primary xylem, and so yields less anatomical detail. The radiating files of secondary tracheids are irregularly split into wedges, but no cellular structure can be seen in the intervening gaps. The secondary xylem tracheids are roundly rectangular in transverse section, and about 70 μm in diameter. Radial and tangential longitudinal sections of the xylem were prepared, but pyritization has destroyed most of the cellular detail. However, from slide V.62040a it appears that the tracheids of both the primary and secondary xylem have scalariform wall thickenings, with minute fimbrials occasionally preserved between the transverse bars.

The coaly surface of this specimen has a finely striated appearance superimposed upon oblique rows of small protrusions, which represent the leaf bases. There are no indications of leaf scars as would be found on all other described genera of lepidodendrolean stem compressions as well preserved as this. There is considerable variation across the coaly surface in the morphological detail observed, but in some areas there appear to be overlapping, linear laminae showing single, central midribs (Fig. 20). It is these laminae which give the specimen its finely striated appearance. Since some of the laminae taper, towards one end of the specimen only, and may appear in spiral arrangement, these structures are interpreted here as retained leaves. No leaf apices are visible. That these are surface features of a leafy stem is supported by the preparation of cuticular samples. Cuticles were obtained by oxidation of pieces of coaly matter with Schulze's solution, clearing in dilute ammonium hydroxide, washing in hydrofluoric acid, and mounting unstained in glycerine jelly.

There is considerable variation in the quality of epidermal anatomy visible in these cuticular preparations from the Carruthers specimen, and in many instances fine cracks hinder detailed observations. Thus, although no ligule pits were obtained, it cannot be concluded that this



18



18a

Figs 18–18a *Anabathra pulcherrima* Witham, emend. herein. Westphalian; Yorkshire. V.62037. Both scale bars represent 10.0mm. Fig. 18, surface view of stem showing 'ulodendroid' scars of lateral branchlet abscission, and striated appearance due to persistent leaf laminae overlying spirally arranged leaf bases; coated with ammonium chloride. Fig. 18a, view of transverse section of same stem, showing permineralized xylem between coalified surfaces. The cortical cavity has been filled with shale.

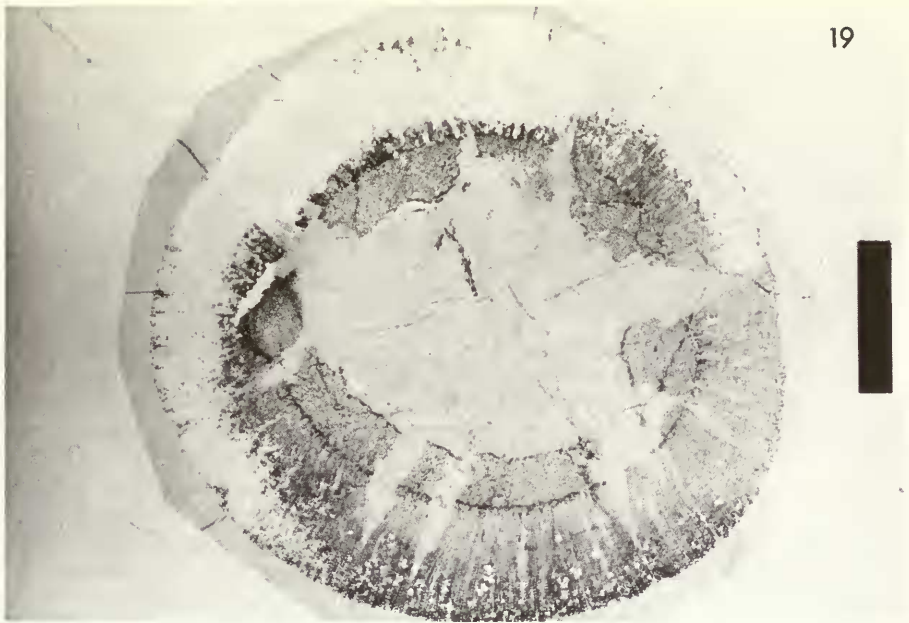


Fig. 19 *Anabathra pulcherrima* Witham, emend. herein. A peel of the permineralized xylem of specimen illustrated in Fig. 18. Note the central medullary cavity, and the smooth boundary between primary and secondary xylem. Pyritization of part of the outer, secondary xylem has destroyed much of the anatomical detail. V.62038a. Scale bar represents 5.0 mm.

plant was necessarily eligulate. A fragment of leaf base cuticle which does show certain details is shown in Fig. 21. The periclinal walls of the epidermal cells are flat and smooth. The anticlinal walls are straight or slightly curved, smooth, and about $1.5\ \mu\text{m}$ to $2.0\ \mu\text{m}$ thick. Stomata occur in apparently random orientation, and at a frequency of about 350 per mm^2 . The cuticular

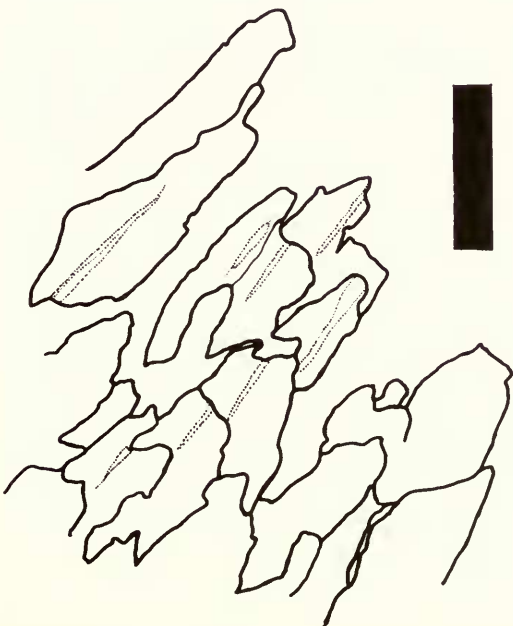


Fig. 20 *Anabathra pulcherrima* Witham, emend. herein. Detail of part of surface of specimen in Fig. 18. Note apparently truncated laminae, some with indications of a central midrib. Some of these slightly tapering laminae appear to be in oblique rows. V.62037. Scale bar represents 6.0 mm.

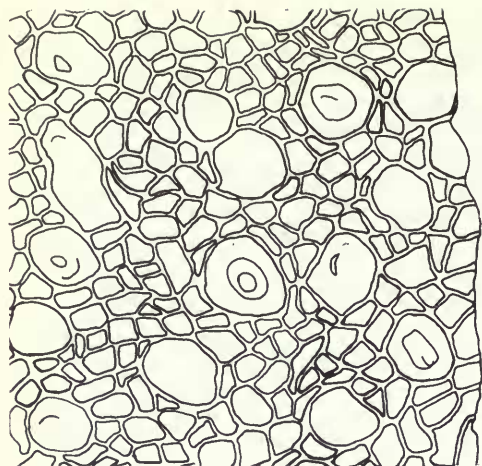


Fig. 21 *Anabathra pulcherrima* Witham, emend. herein. Detail of a cuticle preparation from a leaf base of specimen illustrated in Fig. 18. Note the stomatal pores, indistinctly separated guard cells, and abutting stomatal complexes. V.62037a. Scale bar represents 40 μm .

features of the guard cells appear in focus in the same plane as those of the other epidermal cells. The size and shape of the guard cells is variable, but most are about 40 μm long. Guard cells surrounding different pores are occasionally in direct contact with each other. There is no apparent longitudinal separation of the guard cells as seen from this cuticle. It seems unlikely that there was only one guard cell completely surrounding the stomatal pore, as in the Devonian psilopsid *Zosterophyllum* (Lele & Walton, 1961). All other known lycopsid stomata have two guard cells per pore. It is probable that the cuticle of the guard cells was thinner and no visible flange has been preserved at the junction of these cells. In some cases a rounded pore can be seen at the centre of the guard cells, surrounded by a zone of cuticle about 25 μm long and 15 μm broad. The stomatal pores have been preserved open, and this is evidently so in many of the stomata figured by Graham (1935) from several permineralized lepidodendrolean leaves, including those of *A. pulcherrima* (his 'Type A'). The zone of cuticle immediately surrounding the pore shows no longitudinal division, in common with the remainder of the guard cell cuticle. Although clearly preserved in only a small number of stomatal structures, the features of the central pore and immediately surrounding zone of cuticle appear sufficiently regular such as not to have been much affected by degradation in the life of the plant, during its preservation, or by the preparation procedure. Possibly this zone and the pore were slightly sunken below the level of the remainder of the guard cell surface in life, but there is no great distinction of these levels as seen optically. Since some compression of the cuticle has occurred both vertically and obliquely, no detailed interpretation of the three-dimensional arrangement of cells around the stoma is offered here.

In all these cuticular features there are many similarities to the cuticles described as *U. majus* (Thomas 1967) and *U. landsburgii* (Thomas 1968). The size of the guard cells of the specimen described here compares more closely with *U. landsburgii*, but the stomatal frequency on its leaf bases is intermediate between that found in these two forms. Thomas (1966) concluded that, in general, lepidodendrolean species can be distinguished using cuticular characters, but that generic delimitation of compression specimens still rests more on gross morphology. The external, megascopic details of the two *Ulodendron* species described by Thomas lend further support in correlating that genus with the Carruthers specimen (Fig. 18) described here. He described specimens of *U. majus* and *U. landsburgii* as having leaf laminae retained on quite large pieces of isolated cortex. As mentioned above, there is some difficulty in comparing the inner surface of cortical fragments with the outer surface of the specimen described here. These two named species of *Ulodendron*, *sensu* Thomas, are therefore here considered congeneric, but not conspecific, with *A. pulcherrima*.

The Carruthers specimen showing mixed preservation described here (Fig. 18) is identified as *Anabathra pulcherrima* Witham, since it compares closely with that species in xylem anatomy

and surface morphology, and differs from it in no visible features. The emended diagnoses given above retain *Anabathra landsburgii* (Kidston) comb. nov. and *A. thomasiana* sp. nov. as separate species on the basis of the shapes and stomatal frequencies of their leaf bases. From so few specimens, representing only the three species of *Anabathra* as yet recognized in the compression state, such diagnoses may well be provisional, our knowledge of the specific variations in size and form of both leaf bases and epidermal cells being so restricted. However, it seems preferable at present to retain these specific distinctions while awaiting further data.

The 'whole plant' of *Anabathra*

The name *Anabathra pulcherrima* as used here is taken to apply strictly to certain branching, leafy stems only. There is as yet no evidence for organic connexion between this specific organ and its reproductive or rooting structures. However, as has become common usage with more completely reassembled plants such as the 'Caytonia plant' or the 'Cordaites plant', the expression 'Anabathra plant' seems the most appropriate for describing this lycopsid with its intact body reconstructed, the generic name of the stem being the oldest name given to any distinctive part of it.

DiMichele (1980) indicated the frequent association between *A. pulcherrima* and the bisporangiate cones now called *Flemingites* Carruthers in the permineralized state. In the Lower Carboniferous of Scotland, as mentioned above, one particular cone species associated with *A. pulcherrima* is *F. scottii*. Since it produces megaspores which would be attributable to *Lagenicula subpilosa* as a dispersed spore, this cone species differs from the cones *F. diversus* (Felix) Brack-Hanes & Thomas and *F. schopfii* (Brack) Brack-Hanes & Thomas, which are associated with *A. pulcherrima* in North American coal balls of Pennsylvanian (Upper Carboniferous) age. There are, of course, several other species of *Flemingites*, both compressions and permineralizations, which are not so closely associated with *A. pulcherrima*. Thus, permineralized cones from Roannais and Esnost in the Viséan of France (Galtier 1970), now referred to *Flemingites* sp., are associated with stems named *Lepidodendron rhodumnense* or *L. esnostense* at these localities rather than with *A. pulcherrima*. (However, the assignment of these stems to *Lepidodendron*, sensu DiMichele (1983), is debatable, and they may prove closer in generic affinity to *Anabathra*—see below).

Nothing is known directly of the rooting organ bearing the stem of *A. pulcherrima*. As mentioned above, no roots or rhizophores are preserved in the limestone at Allanbank. However, stigmarian rhizophores and rootlets are known from the Pettycur Limestone and these possibly formed the supporting rhizophores for *Anabathra*. Another lepidodendrale stem, *Lepidophloios scottii*, also occurs in the Pettycur Limestone, but because of its greater rarity at that site, it is unlikely that all the stigmarian axes belonged to *L. scottii* rather than to the much more abundant stems of *A. pulcherrima*. This point is of significance in the ordinal classification of *Anabathra* given below. (In certain coal ball floras dominated by *A. pulcherrima*, DiMichele has observed *Stigmaria* with *Anabathra*-like periderm—personal communication.)

Suprageneric taxonomy of *Anabathra*

One of the most widely accepted and used systems of classification for both fossil and living lycopsids is that proposed by Chaloner & Boureau (1967). Table 1 displays the main features used by these authors to characterize the lycopsid orders which they recognized; the 'A. pulcherrima plant' as described above is included for comparison. Although there is some uncertainty over the form of rooting organ supporting the *A. pulcherrima* stem, it appears that this plant shows greatest similarity to the Lepidodendrales. The only character in which it differs from that order as represented in Table 1 is in its lack of scars of foliar abscission. Hence it seems reasonable to remove emphasis from foliar abscission as an apomorphy or distinctive feature for that lycopsid order, to allow the incorporation of the 'A. pulcherrima plant'. This has, of course, been the ordinal designation already given to *A. pulcherrima* and *F. scottii* under their commonly used synonyms as species of *Lepidodendron* and *Lepidostrobus* respectively.

Table 1 Structural comparisons of 'Anabathra plant' with orders of Lycopsidea. + = presence of character, - = absence of character.

	Secondary growth	Leaf scars	Stigmatic rhizophore	Ligule	Leaf bases/cushions	Heterospory	Cone
Drepanophycales	-	-	-	-	-	-	-
Protolpidodendrales	Rare	Rare	-	Rare	+	Rare	-
Lycopodiales	-	-	-	-	-	-	Some spp.
Miadesmiales	-	-(?)	-(?)	+	-	+	+
Selaginellales	Rare	-	-	+	-	+	Most spp.
Isoetales	+	-	-	+	-	+	-
Lepidodendrales	+	+	+	+	Most spp.	+	Most spp.
'Anabathra plant'	+	-	+(?)	+	+	+	+

Eight lepidodendralean families were proposed by Chaloner & Boureau, namely the Pleuromeiaceae, Bothrodendraceae, Cyclostigmaceae, Lepidodendraceae, Sigillariaceae, Lycopodiopsidaceae, Pinakodendraceae, and Lepidocarpaceae. Unfortunately, the characters used to diagnose these families include different organs according to the family in question. This has led to confusion when evidence for reconstruction has indicated, for example, that certain lepidodendracean stems probably bore cones of the Lepidocarpaceae (Thomas 1978). Ideally, the classification of these fossils would follow that of extant lycopsids in being based upon supposedly 'conservative' reproductive features, in conjunction with characters of attached or associated vegetative organs (Meyen 1975). However, with arborescent fossil plants such as the Lepidodendrales, fragmentation and separation of fertile and vegetative organs before preservation has made this procedure difficult or impossible for most specimens. For all but the Lepidocarpaceae, the type genera of lepidodendralean families are characterized by such features as foliar scars or leaf base morphology. The degree to which the circumscriptions of these essentially 'vegetative families' have been improved by evidence of connexion or association with reproductive structures is very variable. Thus, although sigillariacean stems are known to have borne the *Sigillariostrobus/Mazocarpon* form of cones, much less is known with certainty of how the Bothrodendraceae reproduced (Chaloner & Boureau 1967, Stubblefield & Rothwell 1981).

Since compression fossils of lepidodendralean genera are more common and diverse than the mineralized representatives, it is mainly from the surface morphology of *Anabathra* and the spore content of *Flemingites* that comparisons can be made with the established families of that order. The bisporangiate cones of *Flemingites* differ considerably from the separate mega- and microsporangiate cones of the Lepidocarpaceae and Sigillariaceae. In the Lycopodiopsidaceae and Pinakodendraceae the sporophylls are not aggregated to form cones. The Pleuromeiaceae include species which produced either mono- or bisporangiate cones. The Cyclostigmaceae and Lepidodendraceae are known to have produced bisporangiate cones, and this may have been so also for the Bothrodendraceae. However, foliar abscission leaving a leaf scar is characteristic of all stems at maturity in each of the lepidodendralean families so far recognized.

The lack of foliar scars due to leaf abscission in *Anabathra* should now be assessed for its relevance in familial taxonomy. Chaloner & Meyer-Berthaud (1983) proposed a model for the growth and abscission of lepidodendralean leaves in relation to stem growth and position of the leaves on the plant. They suggested that leaves were never abscised from stems for which the ultimate diameter was less than about 10 mm. Such stems would obviously include lateral branchlets and the distal parts of any highly branched lepidodendralean crown. However, given isolated leafy shoots preserved as compressions lacking cuticle, there seems no way of assigning these fossils to particular genera, families or orders of lycopsids. (A comparable problem exists in the taxonomy of similar shoots of Carboniferous and Permian conifers. In that instance, specimens lacking in detail are assigned to the 'catch-all' genus *Walchia*, and a similar solution may be appropriate for small, detached, lycopsid leafy shoots.) Further problems arise when the maturity of the lepidodendralean shoot is considered. Kosanke (1979) has demonstrated that

lepidodendrolean stems much larger than 10 mm in diameter can only rarely be found to have retained very long leaf laminae of the *Cyperites* form. Chaloner & Meyer-Berthaud suggest that such large, leafy stems represent shoots which were still juvenile; they had not yet produced a branching crown as they were still undergoing apogonetic development at the time of preservation (Eggert 1961). Given the presence of branchlets scars, shorter leaf laminae, and the greater abundance of leafy stems of *Anabathra* as here diagnosed, it appears that the retention of leaves by this genus on stems greater than about 10 mm is a feature of the plant at or near the completion of its determinate growth. This view is supported by the feasibility of preparation of cuticles from the leaf laminae of *A. thomasiana* (Thomas 1967) and *A. landsburgii* (Thomas 1968), while no such preparations have been obtained from the *Cyperites* form of lepidodendrolean leaf. In general, leaves that are retained for longer periods have thicker, more resistant cuticles than caducous leaves.

It is on the basis of this kind of leaf lamina retention, in combination with the production of bisporangiate cones, that the lepidodendrolean family Flemingitaceae is here recognized. The following is a list of genera which may be placed in the Flemingitaceae:

Flemingites Carruthers 1865, emend. Brack-Hanes & Thomas 1983 (Type genus).

Lagenicula Bennie & Kidston 1886, ex Zerndt 1934.

Lagenosporites Potonié & Kremp 1954.

Lycospora Schopf, Wilson & Bentall 1944 (*pro parte*).

?*Stigmara* Brongniart 1822 (*pro parte*).

Anabathra Witham 1833, emend. herein.

Brasilodendron Chaloner, Leistikow & Hill 1979.

Lepidodendron, *sensu lato*. (Those species where leaf laminae are retained on mature stems broader than about 10 mm.)

The monotypic genus *Brasilodendron*, Permian compressions of leafy stems from Brazil, is here assigned to the Flemingitaceae instead of to the Lycopodiopsidaceae as proposed by its authors (Chaloner, Leistikow & Hill 1979). Although no cones or fertile organs of any form are known attached to *Brasilodendron pedroanum*, megaspores named *Lagenosporites brasiliensis* (Dijkstra) Trindade are intimately associated with these stems and probably represent the spores of the same plant. This genus of megaspores is known *in situ* only from *Flemingites* cones, and it seems probable that the *L. brasiliensis* megaspores came from such bisporangiate strobili rather than from the disaggregated sporophylls typical of the Lycopodiopsidaceae. Further, Chaloner, Leistikow & Hill (1979) compare *Brasilodendron* most closely to *Ulodendron*, *sensu* Thomas, in its retention of leaf laminae. They separated these two genera, however, on the basis of sigmoid leaf shape and absence of stomata on the leaf bases in *Brasilodendron*, features which also distinguish the latter from *Anabathra* as diagnosed here.

The genera *Lycospora*, *Stigmara* and *Lepidodendron* are flemingitacean only in part, because their present diagnoses allow their inclusion in other lepidodendrolean families also. Brack-Hanes & Thomas (1983) suggested that spores referable to *Lycospora* from wholly microsporangiate cones (i.e. *Lepidostrobus* Brongniart, *sensu* Brack-Hanes & Thomas), have wider equatorial flanges or zonae than do the microspores of *Flemingites*. Further, these authors proposed that the *Lepidostrobus*-derived *Lycospora* show ornamentation on their proximal surfaces usually absent in the *Lycospora* from *Flemingites* spp. However, these differences between microspores do not serve to distinguish all species of the cone genera *Lepidostrobus* and *Flemingites* as Brack-Hanes & Thomas imply in their diagnoses. Thus, for example, Galtier (1970) has shown that the microspores of the Esnost *Flemingites* sp. have zonae as wide as those in the type specimen of *Lepidostrobus ornatus* Brongniart. Further, some of the bisporangiate cones included as species of *Flemingites* by Brack-Hanes & Thomas lack ligules (e.g. *F. brownii*), or do not contain the gula-bearing forms of megaspores (e.g. *F. brownii*, *F. gallowayi*, *F. noei*), and thus do not fall within their diagnosis for that genus of cones. If these particular species are to be retained within *Flemingites*, it would be more appropriate to concentrate on the bisporangiate nature of the whole cones rather than on the exact morphological details of the spores they contain.

Chaloner (1953a) correlated compressions of bisporangiate cones bearing megaspores referable to *Lagenicula horrida* and *Lagenoisporites rugosus* with the stem compressions named *Lepidodendron simile* and *L. acutum* respectively. (These cones are currently named *Flemingites gracilis* and *F. russellianus* respectively.) However, there is some uncertainty regarding the presence of leaf scars on these two species of *Lepidodendron* (Crookall 1964). Although given this generic designation by Nemejc (1947), these two stem species are known as leafy shoots lacking distinct foliar scars, and with no anatomical or cuticular details. Many of the shoots are not large enough to have shed their leaf laminae to show the leaf cushion details characteristic of *Lepidodendron Sternberg sensu stricto*. Similar problems can be found amongst permineralized material, such as with *Lepidodendron rhodumnense* and *L. esnostense* from the Viséan of France. Thus, such leafy shoots might be equally referable to a number of lycopsid orders and genera, such as *Lycopodites*, *Lepidophloios* or *Anabathra* as diagnosed here. Moreover, certain stems assigned to *Lepidodendron* are known both in organic connexion and in frequent association with cones of the lepidocarpacean *Achlamydocarpon* (Leisman & Rivers 1974, DiMichele 1979, 1983). In this way, stems of the Lepidodendraceae are being attributed to the Lepidocarpaceae or Flemingitaceae.

As discussed above, *Stigmara* is in part classified under the Flemingitaceae, as being the probable rhizophore for this along with all the other lepidodendralean families, but the evidence for its inclusion is only circumstantial.

In the megasporangiate cone *Caudatocarpus* Brack-Hanes (1981), both the abortive and functional spores have been assigned to *Lagenicula*. However, this genus of cones seems to be more closely allied to the Lepidocarpaceae than to the Flemingitaceae, since it contains only one functional spore per megasporangium, and the cones were not bisporangiate.

As DiMichele (1980) has commented, it is interesting that although associated with different species of *Flemingites* cones, the permineralized stems of *Anabathra* found in Europe and North America from the early Viséan to the end of the Westphalian (or their American equivalents) vary so little in their anatomy that all have been included in the single species *A. pulcherrima*. The same apparent stability in vegetative structure may be seen for a comparable stratigraphic range in the probable rhizophore of these and other lepidodendralean plants, *Stigmara ficoides*. From the list of flemingitacean genera given above, the stratigraphical ranges for the megascopic and microscopic genera show only partial coincidence. Thus, although all these genera except *Brasilodendron* are known from the Viséan to the Westphalian, *Lycospora*, *Lagenicula* and *Lagenoisporites* have been recorded also from the Devonian (Chaloner 1967). In part, this reflects the greater likelihood of a plant to be preserved as its very numerous and highly resistant spores rather than as its fewer, more fragile and degradable larger organs. These two megaspore genera have no known affinities other than with bisporangiate cones, whereas *Lycospora* is known also from purely microsporangiate cones. Thus, although megafossil evidence is lacking, palynology suggests that the Flemingitaceae may have first occurred in the Upper Devonian.

Preservation and nomenclature of fossil plants

Although a variety of modes of preservation have been recognized (Schopf 1975), and rare combinations or intermediates between these modes found, most fossil vascular plants are known either as compressions/impressions or as permineralizations. These forms of fossilization result from rather different sets of physical and chemical processes, but a given plant organ is obviously susceptible to either. Correlations can be looked for between permineralized and compressed states of an organ by making comparisons such as those based on the following.

Spore or pollen grain contents. Thus, for example, Chaloner (1953b) found that megaspores belonging to the dispersed spore genus *Tuberculatisporites* occur in cones preserved both as compressions, *Sigillariostrobus*, and as permineralizations, *Mazocarpon*. This approach has some value in correlating vegetative organs indirectly. For example, certain leafy stems are

correlated above by their association or organic connexion with cones of *Flemingites*, both in the compressed and permineralized states.

Geographical and stratigraphical ranges. There is, of course, considerable variation in how widely given taxa of fossil plants occur through time and space. Provinciality in vascular floras is particularly evident between the continents of Upper Carboniferous and Permian times. However, the restricted ranges of fossil plants tend to be used more to deny correlations than to give positive identifications. Thus, taeniopterid leaf impressions from the Pennsylvanian (Upper Carboniferous) of North America are unlikely to belong to the Pentoxylales since that order is restricted to the Jurassic of India, Australia and New Zealand.

Superficial features. The scale of details used to compare the surfaces of compressed and permineralized organs ranges from gross morphology to that of epidermal anatomy obtained from cuticles and paradermal sections. *Sphenopteris hoeninghausii* provides an example where pinnule morphology, the presence of glandular hairs, and the 'dictyoxyton' cortex seen in partially decorticated stem compressions can be compared very closely to, if not specifically identified with, the permineralization *Lyginopteris oldhamia* and its associated organs (Scott 1923). It is, of course, more difficult to compare the microscopic details of epidermal anatomy between these preservation states. Many compressions lack cuticles, and even where cuticle is well preserved, it may have been compressed in such a way that direct comparison of cellular details with a permineralized epidermis is restricted. Correlations between leaf cushion features of permineralized and compressed Lepidodendrales have been made for certain species of, for example, *Sigillaria* (Chaloner & Boureau 1967) and *Lepidodendron* (DiMichele 1983).

Organic connexion between permineralized and compressed tissues. As mentioned above, such a combination of preservation states within one specimen is very rare, but an example can be found in the Devonian progymnosperm *Archaeopteris/Callixylon* (Beck 1960). Organic connexion provides, of course, the strongest unequivocal evidence for correlating organs between preservation states, but it is nevertheless dependent upon the quality of preservation.

This list of methods for correlating permineralizations with compressions may not be exhaustive, but it is evident that there are many limitations to the procedures. One great difficulty arises from the use of diagnostic characters for a genus or species that can only be observed in permineralizations. Thus, Benson (1918) emphasized the presence of a subarchesporial pad of parenchyma in the diagnosis of the permineralized cone *Mazocarpon*. In spite of the same form of spores occurring in the compressed cone *Sigillariostrobus* as in *Mazocarpon*, their overlapping stratigraphical and geographical ranges, their similar surface morphologies, and the association of each with stems of *Sigillaria*, the two generic names for these cones have not been strictly synonymized because the parenchymatous pad has not been preserved in the compressions.

Each of the four approaches to correlation outlined above has been used to some degree in comparing *Anabathra* with *Ulodendron*, *sensu* Thomas. None of the first three lines of evidence, taken individually or in combination, would probably provide sufficient evidence for an unequivocal identification of these two generic concepts with each other. However, notwithstanding the quality of preservation, the evidence provided by organic connexion in V.62037 (Fig. 18) surely brings these two genera together.

Classification and nomenclature are two distinct but interacting fields (Jeffrey 1976). Ideally, observations on and opinions about unnamed specimens could produce a classification which would then require the application of names for the chosen taxa. In practice, of course, our knowledge and understanding of fossil plant structure has been in a continuous state of change from the beginning of palaeobotanical studies, and this is reflected in changing taxonomy. In this paper, new lines of evidence are presented strengthening the comparison of *Anabathra* to *Ulodendron*. From the discussion above, it is clear what specimens fall within *Ulodendron*, *sensu* Thomas 1967, but it is debatable whether that sense is the same as *Ulodendron* of Lindley & Hutton 1831, or of other authors. Expressing my own opinion, therefore, *Ulodendron*, *sensu* Thomas, is here regarded as a synonym of *Anabathra* in its emended sense.

Acknowledgements

I am pleased to thank Prof. W. G. Chaloner and Dr C. R. Hill for their encouragement and detailed criticism during the preparation of this paper. Drs W. A. DiMichele and B. A. Thomas kindly read the typescript and I also thank them for their helpful advice.

Photographic assistance was provided by Mr S. Barber (Bedford College, University of London), and by Mr C. H. Shute and the Photographic Unit of the BM(NH). I gratefully acknowledge receipt of a research studentship from the Trustees of the BM(NH).

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